

# CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society

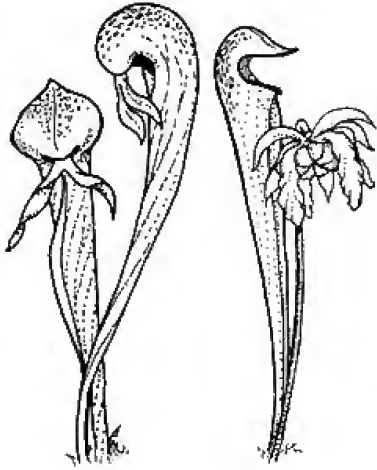
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**December 2009**



Front Cover: The spectacular pitchers of *Nepenthes alba* growing on the upper slopes of Mount Tahan. Photo by Stewart McPherson. Article on page 102.

Back Cover: The opening of a lower/intermediate pitcher of *Nepenthes attenboroughii* growing on the summit of Mount Victoria, Palawan. Photo by Stewart McPherson. Article on page 100.

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## NEWS AND VIEWS:

Francis Brearley (F.Q.Brearley@mmu.ac.uk) writes: It was good to see that the recent discovery of *Nepenthes attenboroughii* (Robinson *et al.* 2009) generated a considerable amount of media interest. Perhaps the most surprising, and indeed slightly worrying, report I read was in the British Daily Mail (19 Aug 2009) which described it as "a grotesque 4 ft tall plant which traps and dissolves rats in a pitcher full of acidic poison". I thought that this kind of reporting of 'exotic' organisms ended in the Victorian era - clearly I was mistaken as sensationalism appears to be alive and well in the British media!

### Reference:

Robinson, A.S., Fleischmann, A.S., McPherson, S.R., Heinrich, V.B., Gironella, E.P., and Peña, C.Q. 2009. A spectacular new species of *Nepenthes* L. (Nepenthaceae) pitcher plant from central Palawan, Philippines. *Botanical Journal of the Linnean Society* 159: 195-202.

## CPN 25 YEARS AGO

Almost two and a half decades ago the Fullerton Arboretum had constructed an artificial bog garden for carnivorous plants. Basically the bog garden consisted of an excavation with plastic lining. In the beginning the Arboretum struggled with maintaining proper water levels and keeping invasive species out. After some experimentation, however, the soil was allowed to partially dry out between waterings. This solved the problems they were having with the constantly waterlogged conditions. In the end the Fullerton Arboretum's artificial bog garden serves as a useful template for carnivorous plant cultivators who would like to have their own artificial bog garden. It is recommended that all of the water should be drained and replaced periodically for non-draining bog gardens so that mineral buildup due to evaporation is avoided. This is important even when distilled or, more commonly, reverse osmosis water is used because the trace minerals left behind by the above processes will inevitably build up.

*NEPENTHES ATTENBOROUGHII:*

A NEW SPECIES OF GIANT PITCHER PLANT FROM THE PHILIPPINES

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Keywords: *Nepenthes attenboroughii*, Mount Victoria, Palawan, Philippines.

In June 2007, I was fortunate to visit the island of Palawan in the south of the Philippine archipelago with two friends and *Nepenthes* experts, Alastair Robinson and Volker Heinrich. We had previously received a report of populations of unknown highland *Nepenthes* from the summit of a little explored peak called Mount Victoria, and after receiving permission from the provincial mayor, we found local hunters who would guide us up the remote mountain to at least as far as they could take us.

On June 21st, after driving as far inland as possible, we began our trek, passing through dense, pristine, lowland rainforest and crossing many rivers into uninhabited and unknown territory. After two days of intense climbing, we reached the upper slopes of the mountain, and as the vegetation became increasingly short, at around 1600 meters (5249 ft) we suddenly saw one great pitcher plant, then a second, then many more. The *Nepenthes* bore spectacular wholly bell-shaped or infundibular lower pitchers (see Figure 1), up to 30 cm (11.8 in) tall and 16 cm (6.3 in) wide, with a volume up to 1.5 liters (1.58 qt). Each lower trap sported yellowish green colouration, generally mottled with dark red or purple colouration on the interior, the lower surface of the lid and on the peristome (see Back Cover). However, most young and newly opened pitchers were pure yellowish green. Our exploration of the summit of the mountain revealed that all populations of the *Nepenthes* occurred in direct sunlight amongst windswept, stunted, upper montane shrubs and scrub 1 metre (3.28 ft) tall or less. Most of the aged, mature plants had formed a rigid, upright or scrambling stem up to 1.5 m (4.9 ft) long, reminiscent of *N. rajah*. We observed that the great pitcher plants continued to the summit of Mount Victoria, which stands at 1726 m (5662 ft), and so all populations naturally experience cool, humid, highland conditions year round.

Unfortunately, one of our guides suffered an injury, and we began our descent of the mountain the following day. But it was nevertheless clear that the *Nepenthes* we had observed represented a new species and was one of the largest pitcher plants known. We had received permission to collect herbarium specimens, and so collected and pressed one of the great pitcher plants. As we descended Mount Victoria over the following two days, the three of us agreed that we would name the new plant in honor of Sir David Attenborough, whose inspirational life works have inspired generations toward a better understanding of the beauty and diversity of the natural world. And so, *Nepenthes attenboroughii* was described in the February 2009 edition of the Botanical Journal of the Linnean Society. The herbarium specimens were deposited at the herbarium of Palawan State University, known by the acronym PPC in Index Herbariorum.

An extensive account of the discovery and morphology of *Nepenthes attenboroughii* is presented in my new, two volume, 1399-page work *Pitcher Plants of the Old World*, which examines all species of *Nepenthes* known worldwide (see [www.redfernnaturalhistory.com](http://www.redfernnaturalhistory.com) for more information).





Figure 1: A newly opened upper pitcher of *Nepenthes attenboroughii*. Note the temporary pure yellowish green colouration. The pitcher is likely to develop purple colouration as it ages. Photo by Stewart McPherson



*NEPENTHES ALBA* AND *NEPENTHES GRACILLIMA*

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Keywords: *Nepenthes alba*, *Nepenthes gracillima*, Mount Tahan, Malaysia, taxonomy, Ridley.

One century ago, the English botanist Henry Ridley traveled to Malaysia and climbed Mount Tahan in (what is now) Pahang. During his climb, Ridley discovered two species of pitcher plants (*Nepenthes*). He described the first one under the name *Nepenthes gracillima* in 1908, and recorded that it produces long, slender pitchers that are predominantly black mottled with green blotches (Ridley 1908). Sixteen years later, Ridley (1924) described the second species which he had encountered on Mount Tahan, and he named that plant *N. alba* for it produces smaller, predominantly white pitchers.

During the one hundred years since Ridley's work, the classification of these two plants has been clouded with errors and confusion. Various botanists have considered the two plants the same species; others mistakenly identified either or both under various incorrect names, including *N. ramispina*, *N. bongso*, and *N. singalana*. Perhaps, as a result of this confusion, *Nepenthes alba* has remained absent from all recent listings of *Nepenthes* species, most notably Clarke (2001) and Rice (2006).

In 2008, I travelled to Mount Tahan to attempt to understand the taxonomy of the *Nepenthes* of that mountain. I observed populations of two distinct types of *Nepenthes* on the upper slopes of Mount Tahan, both of which were consistent with Ridley's original descriptions of *N. gracillima* and *N. alba*. The pitchers of these plants differ in shape, size, and colouration, and they predominantly occur at different altitudes and in distinct habitats. As far as I observed, they do not hybridize or introgress and are easily distinguished from one another. On the basis of my observations, I concluded that Ridley's original classification of these two plants as distinct species is correct, and *N. alba* and *N. gracillima* are indeed different species.

*Nepenthes alba* is named after the Latin *albus* (white). The name refers to the colouration of the upper pitchers of this plant (see Figure 1 and Front Cover). *Nepenthes alba* is widespread across the upper slopes of Mount Tahan, in Taman Negara (Malaysia's largest national park) and it occurs with increasing abundance from 1600 m (5250 ft) altitude to the summit of the mountain, which stands at 2187 m (7175 ft). The population of *N. alba* on Mount Tahan consists of many tens of thousands of plants which display consistent morphology, size, and general colouration (although the upper pitchers vary in colour). The wider distribution of *N. alba* beyond Mount Tahan remains unclear but herbarium specimens from Mount Tapis may represent



Figure 1: The pitchers of *Nepenthes alba* may be pure white.

this species too.

At lower elevations, *N. alba* grows amidst stunted, upper montane forest and scrub, mainly on ridge tops and the upper slopes of the mountain. It produces a branched stem up to 5 m (16 ft) long and scrambles and climbs amidst surrounding vegetation, and mostly grows in strong or direct sunlight. At higher elevations (especially on the upper slopes of Mount Tahan), it grows amidst stunted scrub or in exposed areas, devoid of vegetation, and often forms a compact rosette or short scrambling stem that trails across the ground. On the summit of the mountain, large populations of *N. alba* grow in waterlogged, marshy areas, amidst short marsh grasses and orchids. In such exposed conditions, the *N. alba* plants are greatly dwarfed and flowering specimens just 25 cm (10 in) tall are often observed (see Figure 5).

The lower pitchers of *N. alba* – note the typical purple colouration (see Figure 2). The lower pitchers are up to 12 cm (4.7 in) long and 4.5 cm (1.8 in) wide (although usually are much smaller than these maximum measurements). The bottom half of the pitcher is ovate and slightly swollen. Above this part, the width of the pitcher narrows (usually with a distinct hip) and the rest of the trap is cylindrical or very slightly infundibular towards the pitcher opening. Wings up to 7 mm (0.28 in) wide, fringed with filaments up to 10 mm (0.39 in) long run down the front of the lower pitchers. The peristome is up to 8 mm (0.31 in), and is lined with ribs up to 1 mm (0.04 in) high, spaced up to 1 mm (0.04 in) apart. The peristome is cylindrical and narrow at the front of the pitcher opening, and expanded and flattened at the back (especially below the lid). The peristome ribs are elongated along the inner edge of the peristome and form spikes up to 2 mm (0.08) long, which extend into the pitcher opening. The lid is sub-orbicular or elliptic, up to 4 cm (1.6 in) wide, 3.8 cm (1.5 in) long and lacks an appendage. The spur is generally unbranched and up to 13 mm (0.51 in) long.

The colouration of the lower pitchers is very consistent. The exterior surface of the pitcher is dark purplish brown, often mottled with faint dark purple blotches. The interior of the trap is uniformly light purple, sometimes with faint purple blotches. The lid (both sides) is light purple or reddish. The peristome is dark purple or black.

The upper pitchers are up to 13 cm (5 in) long and 4 cm (1.6 in) wide (although usually are much smaller than these maximum measurements). The bottom half of the pitcher is narrowly infundibular or ovate. Above this part, the width of the pitcher narrows (usually with a distinct hip) and is cylindrical towards the pitcher opening. Wings are reduced to narrow ridges which run down the corners of the flattened front face of the trap. The peristome is up to 7 mm (0.28 in) wide and is slightly expanded at the sides and back of the pitcher opening, or not at all. The peristome is lined with fine ribs up to 0.5 mm (0.02 in) high, spaced up to 1 mm (0.04 in) apart (although often the peristome ribs may be hardly discernable at all). All other parts are consistent with the lower pitchers.

The exterior and interior of the upper pitchers is predominantly white in colour, although the bottom half of the trap may suffuse yellowish green towards the base. Red or pink blotches and flecks are usually present either on the interior or exterior of the upper pitchers (or on both surfaces) although the extent and density of this colouration is extremely variable (see below). The



Figure 2: The lower pitchers of *N. alba* – note the typical purple colouration. Photo by Stewart McPherson



vestigial wing ridges which run down the front of the pitcher may be dark purple or may have no colouration at all in plants which produce pure white pitchers. The peristome is usually pure white, sometimes striped with bands of red, or suffused pinkish. The lid may be pure white, or mottled with red or pink blotches, or suffused reddish.

The colouration of the upper pitchers of this species is extremely variable. From my observations, I would estimate that approximately 90% of *N. alba* plants produce pitchers that are predominantly white with some red or pink blotches on the exterior or interior of the trap. About 9% of the total wild population on Mount Tahan produces upper pitchers which are consistently pure white. The remaining 1% produce upper pitchers that are very heavily lined with red blotches to the extent that they appear predominantly pure red, pink or orange in colour.

*Nepenthes gracillima* derives its name from the Latin *gracillimus* (slenderest or slimmest), which refers to the shape of the upper pitchers (see Figure 3). *Nepenthes gracillima* is currently known only from the upper slopes of Mount Tahan, and it seems to be much rarer than *N. alba*. All known populations (as well as my observations) are recorded amidst upper montane scrub on humid ridge tops between 1600-1700 m (5250-5577 ft) altitude. *Nepenthes gracillima* is not widespread or populous on Mount Tahan, and the populations I observed consisted of just a few dozen plants (but these are consistent and uniform).

*Nepenthes gracillima* readily forms a branched stem up to 3 m (10 ft) long, and scrambles and climbs amidst surrounding vegetation, particularly in areas where it may grow in strong or direct sunlight. In contrast to *N. alba*, *N. gracillima* does not grow on the ground in open, exposed habitat or grow in exposed areas and form stunted, compact foliage.

The lower pitchers are up to 22 cm (8.7 in) long and 7 cm (2.8 in) wide (see Figure 4). The bottom half of the pitcher is ovate and broad. Above this part, the trap narrows slightly (or hardly at all) with a faint hip (or no hip at all) and becomes cylindrical towards the pitcher opening. Wings up to 9 mm (0.35 in) wide fringed with narrow filaments up to 1 cm (0.39 in) long run down the front of the pitcher. The peristome is glossy, up to 1.8 cm (0.71 in) wide, and is narrow at the front of the pitcher opening, but expanded at the sides and back, especially below the lid. A gap a few millimeters wide may be present in the back of the peristome, immediately below the lid. The peristome with conspicuous ribs up to 1.5 mm (0.06 in) high, spaced up to 1.5 mm (0.06 in) apart. The inner margin of the peristome extends into the pitcher opening for several millimeters. The peristome ribs are elongated along the inner edge of the peristome and form spikes up to 2 mm (0.08 in) long, which extend into the pitcher opening. The lid is elliptic or ovate, up to 6 cm (2.4 in) long and 5 cm (2.0 in) wide and lacks an appendage. The spur is usually unbranched and up to 2 cm (0.8 in) long. The exterior of the lower pitcher is predominantly yellowish green, with variable, dark red or purple blotches. The peristome is green or reddish,



Figure 3: An upper pitcher of a plant growing on Mount Tahan that matches Ridley's description of *N. gracillima* – note the morphological differences with the upper pitchers of *N. alba*. Photo by Stewart McPherson



often striped with bands of dark red or purple. The interior of the pitcher and lower surface of the lid are yellowish green or light yellow. The upper surface of the lid is olive green, with variable dark purple or black flecks. In all populations of *N. gracillima* which I observed, the colouration of the lower pitchers was consistent (as described above).

The upper pitchers are up to 26 cm (10 in) long and 5 cm (2 in) wide (many times larger than the typical size of the upper pitchers of *N. alba*). The traps are wholly infundibular, although extremely narrowly so, and greatly elongated. Sometimes, the bottom third of the pitcher may be slightly swollen, with a very faint hip above. Wings are reduced to narrow ridges which run down the corners of the abruptly flattened, angular front face of the trap. The peristome is up to 12 mm (0.47 in) wide and is slightly expanded at the sides and back of the pitcher opening, or not at all. The peristome is lined with fine ribs up to 0.5 mm (0.02 in) high, spaced up to 1 mm (0.04 in) apart (although often the peristome ribs may be hardly discernable at all). All other parts are consistent with the lower pitchers.

The exterior of the upper pitcher is predominantly black, mottled with variable bright green blotches (which are elongated towards the base of the trap). This colouration is also present on the upper surface of the lid, however the lower surface of the lid and interior of the pitcher are light yellowish green. The peristome is yellow, striped with narrow bands of black and purple.

Recent observations of these two spectacular and very beautiful pitcher plant species on Mount Tahan raises many questions as to whether both also occur widely across the many peaks of central Peninsula Malaysia, and beyond. However, since both *N. alba* and *N. gracillima* occur within responsibly and strictly managed protected areas, both are not currently threatened with extinction. Certainly more extensive studies of these two taxa are required to understand their association and taxonomy.

An extensive account of the discovery, taxonomy, and morphology of *Nepenthes alba* and *N. gracillima* is presented in my new, two volume, 1399-page work *Pitcher Plants of the Old World*, which examines all species of *Nepenthes* known worldwide (see [www.redfernnaturalhistory.com](http://www.redfernnaturalhistory.com) for more information).



Figure 4: A lower pitcher of *N. gracillima* – note the profoundly different morphology (and size) in comparison to *N. alba*. Photo by Stewart McPherson

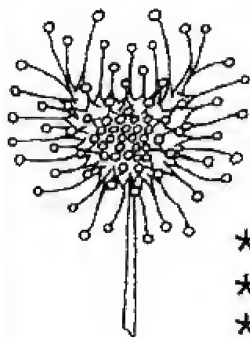


Figure 5: A stunted, flowering, *N. alba* plant growing on the bleak, windswept summit of Mount Tahan. Photo by Stewart McPherson.

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Keywords: chemistry: photosynthesis, *Aldrovanda*, *Utricularia*.

Abstract

Net photosynthetic rate of aquatic carnivorous plants in standing waters can sometimes be limited by low concentration of free CO<sub>2</sub>. As net photosynthetic rate of terrestrial plants growing *in vitro* is greatly reduced, as compared to the same plants grown naturally, it could be assumed that photosynthetic CO<sub>2</sub> affinity in aquatic carnivorous plants growing *in vitro* will be reduced. The aim of this study was to compare values of CO<sub>2</sub> compensation point of photosynthesis in several strains of *Aldrovanda vesiculosa* and in 13 aquatic *Utricularia* species, both in plants growing under nearly-natural conditions in containers or aquaria and *in vitro*. The dependence of CO<sub>2</sub> compensation point on growth conditions is discussed.

Introduction

About 50 species of the genera *Aldrovanda* and *Utricularia* are submerged aquatic or amphibious carnivorous plants (Juniper *et al.* 1989; Taylor 1989; Guisande *et al.* 2007). Aquatic carnivorous plants (ACPs) usually grow in shallow standing dystrophic (humic) waters which are usually poor in inorganic N and P, but commonly also in K (Adamec 1997a). They are rootless and take up all necessary nutrients through their shoots, either directly from water or from prey. Very rapid growth of ACPs in nutrient-poor habitats requires ecophysiological adaptations that enable the plants to gain limiting mineral nutrients. These adaptations include carnivory, efficient nutrient re-utilization (recycling) from senescent shoots, and very high affinity for mineral nutrient uptake from water (Kamiński 1987; Adamec 2000; Englund & Harms 2003).

ACPs in their typical habitats may also face shortage of light (only 2-20% of incident PAR irradiance) and sometimes also free CO<sub>2</sub> (below 0.02-0.05 mM) though CO<sub>2</sub> concentration ([CO<sub>2</sub>]) is commonly high in their habitats, >0.1 mM (*e.g.*, Hough & Fornwall 1988; Adamec 1997b, 2007; Adamec & Kovářová 2006). Therefore, net photosynthetic rate of ACPs in standing waters, like that of other submerged non-carnivorous plants generally, is limited by unfavourable physical and chemical factors which are attributes of the aquatic environment: low diffusion rate of CO<sub>2</sub>, variable [CO<sub>2</sub>] strongly dependent on water pH and total alkalinity (TA), and, also, shortage of light (*e.g.*, Maberly & Madsen 2002). The maximum net photosynthetic rate of ACPs (per unit biomass) is usually higher than that known in aquatic non-carnivorous plants (Adamec 1997b, 2006). It has been shown that *Aldrovanda vesiculosa* and several aquatic *Utricularia* species use only CO<sub>2</sub> for photosynthesis (Moeller 1978; Adamec 1995, 1997b; Adamec & Kovářová 2006). For these species, estimated values of CO<sub>2</sub> compensation point of photosynthesis (CP CO<sub>2</sub>; *i.e.*, CO<sub>2</sub> concentration at which net photosynthetic rate is zero and gross photosynthetic rate equal to respiration) range between 1.5-13 µM. Similar values within 1.4-11 µM have also been reported for aquatic non-carnivorous plants (Maberly & Spence 1983). However, it has recently been found in ecologically very plastic *U. australis* that growth conditions of a very high pH (or negligible [CO<sub>2</sub>]) can even induce a weak HCO<sub>3</sub><sup>-</sup> use (Adamec 2009).

Most species of ACPs grow very rapidly, due to both rapid apical growth and frequent branching (Friday 1989; Adamec 1999, 2000, 2007; Adamec & Kovářová 2006). Their doubling time of biomass can be only within 8-20 days and their apical growth rate within 1-3.5 new leaf whorls or nodes per day. Obviously, their high net photosynthetic rate is a prerequisite for their very rapid growth (Adamec 1997b) as this growth pattern is associated with a significant loss of carbohydrates in senesced shoot segments (Adamec 2000). Therefore, high  $[\text{CO}_2]$  in the water is one of the most important ecological requirements for rapid growth of ACPs (Adamec 1999).

Besides growing in nutrient-poor waters in containers or aquaria, ACPs of both genera can also be grown easily *in vitro* in mineral-rich liquid media supplemented with 2-3% sucrose as an energy source (Adamec & Pásek 2000; Adamec & Kondo 2002). Up to now, 14 *Aldrovanda* strains and 14 aquatic *Utricularia* species have been successfully grown *in vitro* (Pásek & Adamec, unpubl.). It is well-known that net photosynthetic rate of terrestrial plants grown *in vitro* on agar is greatly decreased, as compared to the same plants grown naturally, and that a significant part of this effect is caused by sucrose uptake from media (e.g., Fuentes *et al.* 2005; Fila *et al.* 2006). It can therefore be assumed that net photosynthetic rate and  $\text{CO}_2$  affinity in ACPs growing *in vitro* in liquid media will also be significantly lower than those in the plants growing under nearly-natural conditions. The aim of this study was to compare values of CP  $\text{CO}_2$  in several strains of *A. vesiculosa* and in 13 aquatic *Utricularia* species, both in plants growing under nearly-natural conditions in containers or aquaria and *in vitro*. The dependence of CP  $\text{CO}_2$  on growth conditions (pH,  $[\text{CO}_2]$ ) is discussed.

## Materials and Methods

Experimental ACPs were grown under nearly-natural, dystrophic conditions outdoors either in two large plastic containers of 350 or 700 litres (Adamec 1997c) or in 3-30 l aquaria standing in cooling water in a 1.5-m<sup>3</sup> plastic container, or were grown in a greenhouse in 3-20 l aquaria floating in a 300-l plastic container. Litter of robust sedges (*Carex*) was used as a standard substrate (Adamec 1997c, 1999) and all cultures were partly shaded (usually 20-50% of incident irradiance on the level of plants) and occasionally fed on fine prey. The species grown under these conditions at the beginning of August 2007, to measure CP  $\text{CO}_2$ , are given in Table 1.

The following species growing *in vitro* were used in another run of the experiment: *Aldrovanda vesiculosa* (three strains from E Poland, Hungary, Botswana), *U. stygia* (from the Czech Rep.), *U. bremii* (from NW Russia), *U. reflexa* (from Zambia), *U. inflata* (from NJ, USA), *U. floridana* (from FL, USA), *U. striata* (from NJ, USA), *U. aurea* (from Malaysia), *U. breviscapa*, and *U. hydrocarpa* (both from Nicaragua). *in vitro* plants were grown aseptically in ca. 150 ml of a medium in 0.5-l serological flasks in white fluorescent light ( $15\text{--}40\ \mu\text{mol m}^{-2}\text{ s}^{-1}$  PAR) at a light:dark regime of 14/10 h and at  $19\pm 1^\circ\text{C}$ . A half-strength Gamborg B5 liquid medium with 500 mg l<sup>-1</sup> KNO<sub>3</sub>, microelements, vitamins, and 2.5% sucrose, but without other organic substances (see Adamec & Pásek 2000), was used for growing the plants for 3-5 weeks. The initial pH of the medium before autoclaving was ca. 5.5. Each species of ACPs was usually available in 2-3 flasks. Before the experiment, the bulk of the medium was more or less loosely overgrown by plant biomass. In species forming two types of shoots (carnivorous and photosynthetic; *U. stygia*, *U. striata*, *U. floridana*), the proportion of greenish carnivorous shoots with traps was very low, by guess <5-10%. In most species but *U. hydrocarpa* and *U. breviscapa*, the shoots were freshly green, while in these two species, shoot bases were yellowish.

The plants from containers or aquaria or *in vitro* cultures were washed thoroughly by tap water and cleaned of sessile organisms. For estimation of CP  $\text{CO}_2$  using the final-pH method (Maberly & Spence 1983), apical parts of 1-3 shoots about 6-7 cm long (or 3-15 shoots 3-8 cm long in *in vitro* plants) were put in 10-ml test-tubes in the solution of 1 mM NaHCO<sub>3</sub> + 0.1 mM KCl (pH ca. 7.65; Adamec 1995; Adamec & Kovářová 2006). The whole internal volume was filled evenly with the plants. Air volume of about 1 ml was let in the closed tubes to reduce the final  $[\text{O}_2]$  in the solution. The tubes with plants were exposed to natural light in water at 21-25°C and ca. 300-450  $\mu\text{mol m}^{-2}\text{ s}^{-1}$  PAR for 5 h and final-pH values were measured. Values of CP  $\text{CO}_2$  were cal-



culated from pH and TA after Helder (1988). All measurements were performed in five replicates.

For a calculation of [CO<sub>2</sub>] in culture waters, pH and TA were measured in each aquarium or container at the time of plant sampling. pH was also measured in used *in vitro* media from which the experimental plants were taken. pH values were used as such and were not transformed. Mean values ±1SE intervals are shown. Statistically significant differences between the same species were evaluated by a two-tailed Student t-test. Linear regression models were used to find statistically significant meaningful relationships between variables. Three important linear regressions at p<0.05 are shown in Table 2. For this aim, results for various *Aldrovanda* strains and *Utricularia* species were pooled together as both groups behave ecologically in the same way (*e.g.*, Adamec & Kovářová 2006).

Species (accession)	Plants from containers or aquaria				Plants <i>in vitro</i>	
	pH	TA (meq l <sup>-1</sup> )	[CO <sub>2</sub> ] (μM)	CP CO <sub>2</sub>	pH <i>in vitro</i>	CP CO <sub>2</sub> (μM)
<i>A. vesiculosa</i> , E Poland	7.72	1.51	67	6.25±0.47	3.68-3.73	4.24±0.15*
<i>A. vesiculosa</i> , Hungary	8.67	0.71	3.4	1.90±0.15	3.11-3.28	5.15±0.29*
<i>A. vesiculosa</i> , SE Australia	8.56	0.78	4.9	2.87±0.19	--	--
<i>A. vesiculosa</i> , Botswana	7.66	0.61	31	3.09±0.19	3.83-4.04	5.95±0.47*
<i>U. stygia</i> , Czech Rep.	8.11	1.49	27	3.08±0.20	3.21-3.35	5.72±0.33*
<i>U. vulgaris</i> , Czech Rep.	8.11	1.49	27	7.09±0.61	--	--
<i>U. intermedia</i> , Czech Rep.	7.49	0.79	60	3.60±0.17	--	--
<i>U. bremii</i> , NW Russia	7.49	0.79	60	4.38±0.28	--	--
<i>U. bremii</i> , S Bohemia	8.33	1.25	13	2.45±0.16	3.19-3.21	8.49±0.34*
<i>U. reflexa</i> , Botswana	7.66	1.02	52	4.04±0.09	--	--
<i>U. reflexa</i> , Zambia	7.91	0.54	15	4.57±0.23	3.11-3.50	8.75±0.61*
<i>U. inflata</i> , NJ, USA	7.66	1.02	52	8.31±0.81	3.08-3.25	4.52±0.25*
<i>U. purpurea</i> , FL, USA	8.57	1.55	9.4	3.70±0.34	--	--
<i>U. floridana</i> , FL, USA	7.86	1.23	40	13.6±1.94	6.13	2.53±0.08*
<i>U. striata</i> , NJ, USA	6.79	0.54	205	7.38±0.62	5.14-5.41	3.07±0.08*
<i>U. aurea</i> , Malaysia	7.26	0.79	102	4.66±0.67	3.08-3.17	3.67±0.25 <sup>NS</sup>
<i>U. dimorphantha</i> , Japan	6.60	0.76	449	9.74±0.54	--	--
<i>U. breviscapa</i> , Nicaragua	--	--	--	--	3.36-3.37	5.04±0.75
<i>U. hydrocarpa</i> , Nicaragua	--	--	--	--	4.35-5.07	147±35

Table 1: Comparison of compensation points of CO<sub>2</sub> (CP CO<sub>2</sub>) of aquatic carnivorous plants grown under nearly-natural conditions in containers or aquaria, with those for plants growing in *in vitro* in a mineral medium with 2.5% sucrose for 3-5 weeks. pH and TA in the water are shown for the plants from containers or aquaria; the pH range of used *in vitro* media is shown (1-3 flasks). Means±SE are shown; n=5. Statistically significant differences between the same species or strains, \*, p<0.01; NS, non-significant, p>0.05.

No.	Linear regression model	r <sup>2</sup>	p
1	CP CO <sub>2</sub> (w) = 25.1 – 2.61 pH	0.47	0.003
2	CP CO <sub>2</sub> (w) = 3.74 + 0.015 [CO <sub>2</sub> ]	0.52	0.002
3	CP CO <sub>2</sub> (w) = 11.2 – 1.09 CP CO <sub>2</sub> (iv)	0.42	0.044

Table 2: Linear regression models between variables showing all statistically significant (p<0.05) meaningful correlations; (w), for plants from dystrophic waters in containers and aquaria; (iv), for *in vitro* plants; n=10-16; r<sup>2</sup>, coefficient of determination; p, probability level.

### Results and Discussion

ACPs used for this study grew in containers and aquaria under very different pH and CO<sub>2</sub> conditions, while TA values were relatively stable (Table 1). Overall, pH ranged between 6.6 and 8.7 and [CO<sub>2</sub>] between only 3.4 and 450 µM. Co-occurring filamentous algae could have a certain influence on higher pH and lower [CO<sub>2</sub>] but their influence was not tested. Though pH and [CO<sub>2</sub>] presumably mildly oscillated in the containers and aquaria during day and night time, only one estimation of these parameters was performed before plant sampling but it gave reliable information on growth conditions. Values of CP CO<sub>2</sub> in 17 plant strains or species from nearly-natural cultures ranged between 1.9-13.6 µM (mean 5.3±0.7 µM) and about the same values between 2.5-8.8 µM (mean 5.2±0.6 µM) were found in all 11 *in vitro* strains or species but *U. hydrocarpa*. The *in vitro* culture of the latter species was more aged than in all other species and its values of CP CO<sub>2</sub> were as great as 147±35 µM. pH values of used *in vitro* media ranged between 3.08 and 6.13 but they were usually within only 3.2-4.0 (Table 1); the difference between parallel flasks for each species was usually only 0.1-0.3 pH due to a relatively higher buffering capacity of the medium. Linear regression models (*U. floridana* as an outlier was excluded) revealed a highly significant correlation between the values of CP CO<sub>2</sub> of APCs grown in containers or aquaria and between pH in these waters (Table 2, No. 1). As these pH values correlated very strongly r<sup>2</sup>=0.64; p=0.00011; data not shown) and negatively with [CO<sub>2</sub>] in the waters, CP CO<sub>2</sub> of APCs correlated also highly significantly with [CO<sub>2</sub>] (No. 2). Except for *U. aurea*, the values of CP CO<sub>2</sub> within each of all other 9 ACP strains or species growing under *in vitro* and nearly-natural conditions were highly significantly different (Table 1). Yet, a significant correlation was found between these values of CP CO<sub>2</sub> for all 10 strains or species (Table 2, No. 3).

It follows clearly from the results (Table 1) that different *Aldrovanda* strains and 11 *Utricularia* species, regardless of their geographic origin, behave photosynthetically as typical, strict CO<sub>2</sub> users (cf. Maberly & Spence 1983). Evidently, there was no difference between *Aldrovanda* strains and *Utricularia* species on one hand and between *Utricularia* species with monomorphic and dimorphic shoots on the other. Based also on all literature data available (Moeller 1978; Adamec 1995; Adamec & Kovářová 2006), it may be concluded that all ACP species are strict CO<sub>2</sub> users. The recent finding of a weak HCO<sub>3</sub><sup>-</sup> use in *U. australis* growing at a very high pH (Adamec 2008) may be a very rare exception from this rule and does not contest much this generalization. Within the ecological group of ACPs, the ecological strategy of a strict CO<sub>2</sub> use is consistent with relatively high [CO<sub>2</sub>] which commonly occurs at most of natural sites of ACPs (Adamec 1997a, 1997b). In aquatic non-carnivorous plants, values of CP CO<sub>2</sub> depend markedly on concentration of inorganic carbon, mainly of CO<sub>2</sub>, in the ambient water and this relationship also holds for strict CO<sub>2</sub> users (Madsen *et al.* 1996); low [CO<sub>2</sub>] leads to low values of CP CO<sub>2</sub> and vice versa. The same adaptational relationship has also been confirmed for ACPs (Table 2, No. 2). Therefore, the differences in CP CO<sub>2</sub> found between the species can be attributed to differences in [CO<sub>2</sub>] during the growth of the plants rather than to interspecific differences alone. Thus, a more efficient CO<sub>2</sub> uptake is induced by a shortage of CO<sub>2</sub> or a higher pH value. Nevertheless, when ACPs grow under the conditions of a marked CO<sub>2</sub> limitation this ecologically unfavorable factor can also be alleviated by prolifically catching prey and absorption of organic carbon from prey (Adamec 1997a, 1999). Anyway, shortage of CO<sub>2</sub> leads to a significant decrease in apical shoot growth



rate as found in *Aldrovanda* (Adamec, unpubl.).

Although the physiological age of the *in vitro* cultures of ACPs used was partly different due to different depletion of the media, the pH values in used media in most species (except for *U. floridana* and *U. striata*) were well below 5.0 and usually only 3.2-4.0 (Table 1). Such low pH values in a half-strength Gamborg B5 media were also reported by Adamec & Pásek (2000) and Adamec & Kondo (2002) for *Aldrovanda* cultures. As follows from the cited studies the very low pH in used Gamborg B5 media reflects the availability of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in the fresh media as well as a great uptake preference for  $\text{NH}_4^+$  over  $\text{NO}_3^-$  (Adamec 2000; Adamec & Pásek 2000). Thus, it is possible to suggest that *U. floridana* and *U. striata* take up also a considerable proportion of  $\text{NO}_3^-$  which leads to medium alkalization.

The fact that CP  $\text{CO}_2$  values in *in vitro* plant species are comparable with those in the plants growing under nearly-natural conditions (Table 1) testifies that the former group of plants is able to normally photosynthetically use  $\text{CO}_2$ , with a  $\text{CO}_2$  affinity common for the latter group. Yet, these results do not show how great net photosynthetic rate of these *in vitro* raised plants can be as compared to nearly-natural cultures. To our knowledge, no similar measurement of CP  $\text{CO}_2$  has been conducted in aquatic non-carnivorous plants *in vitro* so far and, thus, our data cannot be compared. However, *U. hydrocarpa* grown *in vitro* exhibited weak symptoms of senescence and its CP  $\text{CO}_2$  was enormously high ( $147 \pm 35 \mu\text{M}$ ). It is therefore possible to assume that the physiologically older a culture was, the higher was its CP  $\text{CO}_2$ . In terrestrial non-carnivorous plants growing *in vitro* with sucrose, net photosynthetic rate per unit leaf area is only about a half of that measured in the same species under *ex vitro* conditions (Fila *et al.* 2006) and sucrose added to the medium can reduce net photosynthetic rate by 30-45% (Lucchesini *et al.* 2006). Although the values of CP  $\text{CO}_2$  in nearly-naturally grown ACP species depended strongly on the ambient  $[\text{CO}_2]$  they also correlated significantly with those *in vitro* (Table 2, No. 3). This might indicate that certain interspecific differences in CP  $\text{CO}_2$  among the species or strains do exist.

It should be noted that the *in vitro* *Utricularia* species looked quite different than the plants from the nearly-natural cultures. The former group of plants had relatively abundant but small traps the maximum size of which did not extend 1.5 mm (or 2.5 mm in *U. reflexa*; see Figure 1), while the latter plant group had much larger traps (usually 2-4 mm, but up to 7 mm in *U. reflexa*; see Figure 2). It is possible to assume that the proportion of trap biomass to the total plant biomass (*i.e.*, investment in carnivory) is much lower in grown aquatic species than in the same



Figure 1: *Utricularia reflexa* (a clone noted as having relatively large traps) from Zambia grown under nearly-natural conditions in outdoor aquaria. Scale bar indicates 10 mm; the largest trap size is 7 mm; September 2007. Photograph by Lubomír Adamec.

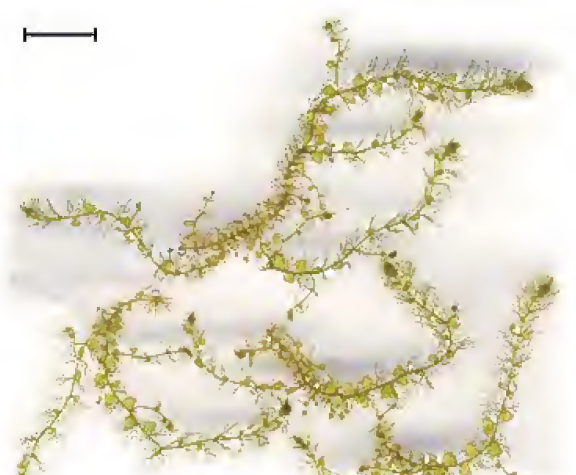


Figure 2: The same Zambian clone of *U. reflexa* as shown in Figure 1 grown *in vitro*. Scale bar indicates 10 mm; the largest trap size is only 2.5 mm. Photograph by Lubomír Adamec.

species grown in nearly-natural cultures. Thus growing ACPs in concentrated mineral media with sucrose presumably causes great changes (decrease) of investment in carnivory.

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THE NATURAL BEHAVIOR OF *DROSERA*:  
SUNDEWS DO NOT CATCH INSECTS ON PURPOSE

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*D. rotundifolia*.

Abstract

The trapping behavior of carnivorous plants has attracted attention of naturalists for almost two centuries. With the most observations made in laboratories, the behavior of sundew *in situ* has not been studied enough. We observed *Drosera* leaf behavior in natural habitats with non-manipulative technique. Three leaf characteristics for two species (*D. rotundifolia* L. and *D. anglica* Huds.) from two regions (6 plants with 30 leaves) were continuously observed during 196 hours. Our observations show that changes of the leaf characteristics of two sundew species in nature are almost casual and likely only corrected by external factors such as relative air humidity and presence of fresh prey (“semi-accidental feeding”). We consider trapping leaves of the two studied *Drosera* species as transitional structures between active and passive fly-paper traps.

Introduction

The origin and evolution of carnivory is an important and challenging topic in evolutionary ecology (Benzing 1987). However, the origin of carnivory can hardly be studied in animals since this group is likely ancestrally carnivorous (Nielsen 1995). Carnivorous fungi and plants are more applicable for that research. Among the carnivorous plants, sundews (*Drosera*, Droseraceae) represent an interesting example where, according to experimental data and morphology of some species, both active active and passive prey catching are possible (Juniper *et al.* 1989).

Most of the research of sundew behavior have been done in laboratories, from the early studies (Kellerman & Raumer 1878; Busgen 1883) to those conducted in recent times. Experiments usually show that, for some species of sundews, if prey provides sufficient stimulation, all leaf tentacles bend inwards and cover the prey with an enzyme-containing slime. Upon stimulation with the prey, there is a (1) rapid movement of tentacles in the first 10-30 seconds after touching and (2) slow movement by tentacles that were not at first in contact with prey. This slow movement is observed within first hour after initial contact (Hooker 1916). Juniper *et al.* (1989) state that sundews also secrete a slime just as the prey is captured. After the initial slime secretion, the edge of the leaf blade slowly bends and covers the captured prey. When the digestion process has ended, the leaf blade unwraps, the tentacles straighten and the slime dries (Hooker 1916).

Unfortunately, only several uncoordinated short observations on sundews (Treat 1873; Canby 1874) were conducted in natural habitats. Therefore, the differences between laboratory, artificial conditions, and conditions *in situ* may affect the observations. For example, factors such as weather (Gomez 1998), edaphic conditions, prey amount available, type of prey, and kleptoparasitism by ants (Thum 1989a) cannot properly be taken into account in the indoor experiments.

Several observational strategies are available for outdoor experiments. We choose the most non-manipulative one which is referred below as “continuous observations”. The team of observers recorded



several parameters every 30 or 40 min. All watchers were trained to make consistent observations. The first review of results from one species (*D. rotundifolia*) already suggested that the *in situ* natural behavior of sundews may be radically different from laboratory behavior (Volkova & Shipunov 2005). However, at that time we did not process our data statistically, and all observations were restricted to one species.

Different sundew species may differ in feeding behavior. As an example, significant inter-specific differences of prey amount that remained on the leaf in 24 hours were revealed in the field experiments (Thum 1988, 1989a,b) with artificial feeding of trapping leaves of *D. rotundifolia* and long-leaved *D. intermedia* Hayne. Mire ants carry away about two thirds of prey from trapping leaves of *D. rotundifolia*, while prey on the leaves of *D. intermedia* remain almost untouched (Thum 1989b). *Drosera rotundifolia* is reported to catch three times more prey than *D. intermedia* (Thum 1989a,b). In the north of European Russia, *D. rotundifolia* grows together with *D. anglica*, another long-leaved sundew species that is similar to *D. intermedia* both morphologically and ecologically (Webb 1993). Therefore, *D. anglica* seems to be a good choice for expanding our methods to a larger number of species. We also decided to process our data in a much more detailed way than in our previous work (Volkova & Shipunov 2005).

## Materials and Methods

To expand the taxonomic coverage of our research, we observed plants of *D. anglica* in natural habitats in Loukhi district of Karelia republic (Northern Karelia, European Russia) on July 16-18, 2005. Plants were growing on the *Sphagnum* mire on the shore of an unnamed lake (N66° 18.5', E33° 07.5'), and were chosen randomly from a typical population. Each of two chosen plants possessed 7 trapping leaves, therefore there were 14 observational units. Continuous observations for these two plants lasted for 52 hours. At 40 minute intervals we recorded (1) secretion degree, (2) bending degree of marginal tentacles, and (3) shape of each leaf (Volkova & Shipunov 2005; see also Table 1). We also counted the number of prey units on the leaf blade and measured relative air humidity with a common digital psychrometer located nearby.

Observation *in situ* is usually a challenge. In particular, we did not use video cameras since it is hard to organize work with cameras in a non-threatening way. Instead, we employed teams of observers. To avoid problems involved with human observers, each team was trained to reach the satisfactory level of consistency. All teams employed in 2000, 2002, and 2005 were led by the same supervisors who controlled quality of observations. The scales (Table 1) were designed to be simple enough, which eased the learning curve.

For the analysis, we also used data from our observations on *D. rotundifolia* (Volkova & Shipunov 2005). These observations were performed in North Karelia (nearby location) in 2000, and in Tver region (Middle Russia) in 2002. In all, 4 plants and 16 observational units were observed. Observations in North Karelia and in Tver region continued for 72 hours each (once in approximately 40 min and once in 30 min respectively).

For each leaf in the *D. anglica* and *D. rotundifolia* data, we created graphs of changes of all the three leaf characteristics during the observation time. The most typical graphs are presented in Figures 1-3.

All data were analyzed mostly with non-parametric statistical methods. Leaf reaction to the prey was examined using Wilcoxon tests, comparing the characters of leaf in the moment of prey capture and in the given time shift (0.5, 1, 2, and 3 hours). Wilcoxon tests were also employed to compare the observed leaf behaviour with the expected behaviour, predicted from the literature data of indoor experiments (Hooker 1916; Juniper *et al.* 1989), and to compare leaves with the absence of prey with leaves having the prey after 1 h interval. Concordance of changes of different characters of the given leaf as well as concordance between leaves of one plant was checked with Spearman correlation test. This test was also employed to reveal the dependence of different leaf characters on air humidity. Chi-square tests were used to understand the significance of the amount of leaves with characteristics unexpected from the literature. Finally, ANOVA were used for revealing the relationship between leaf characteristics and air humidity, for analysis of the dependence between time shift and leaf characteristics, and for the analysis of coordination between different leaves of the same plant.

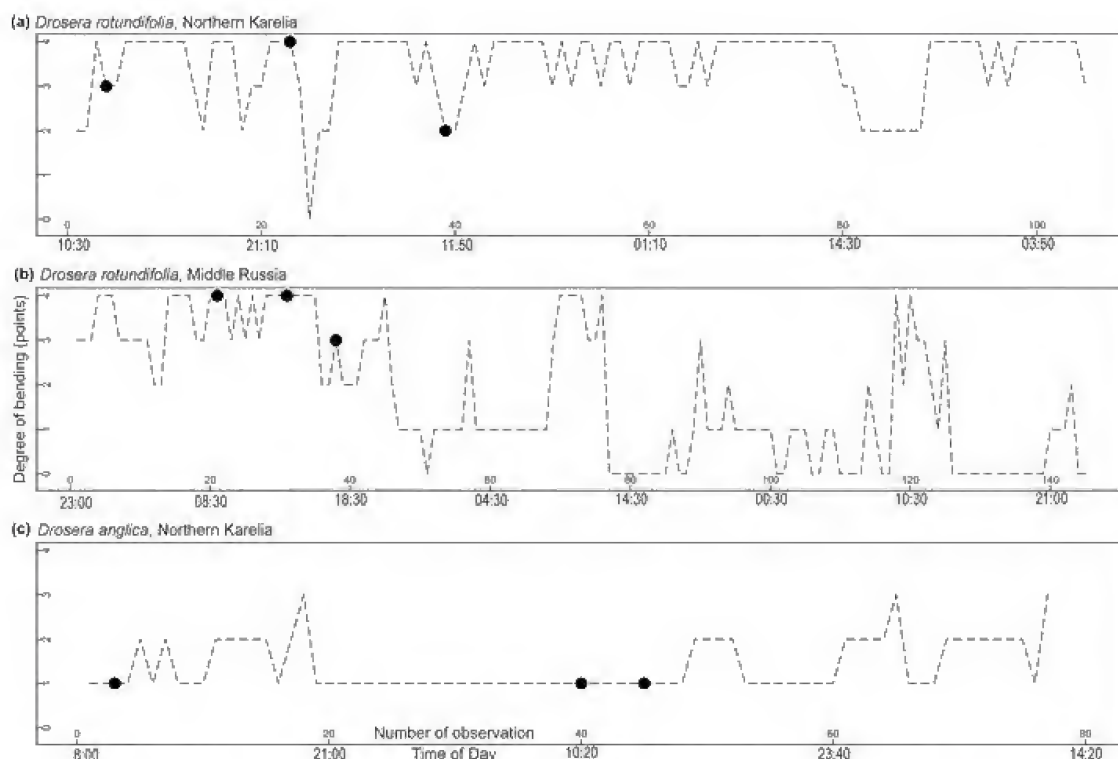


Figure 1: Changes in the degree of bending of marginal tentacles of model *Drosera* leaves. The times of arrival of the fresh insect on the leaf blade are shown with filled circles.

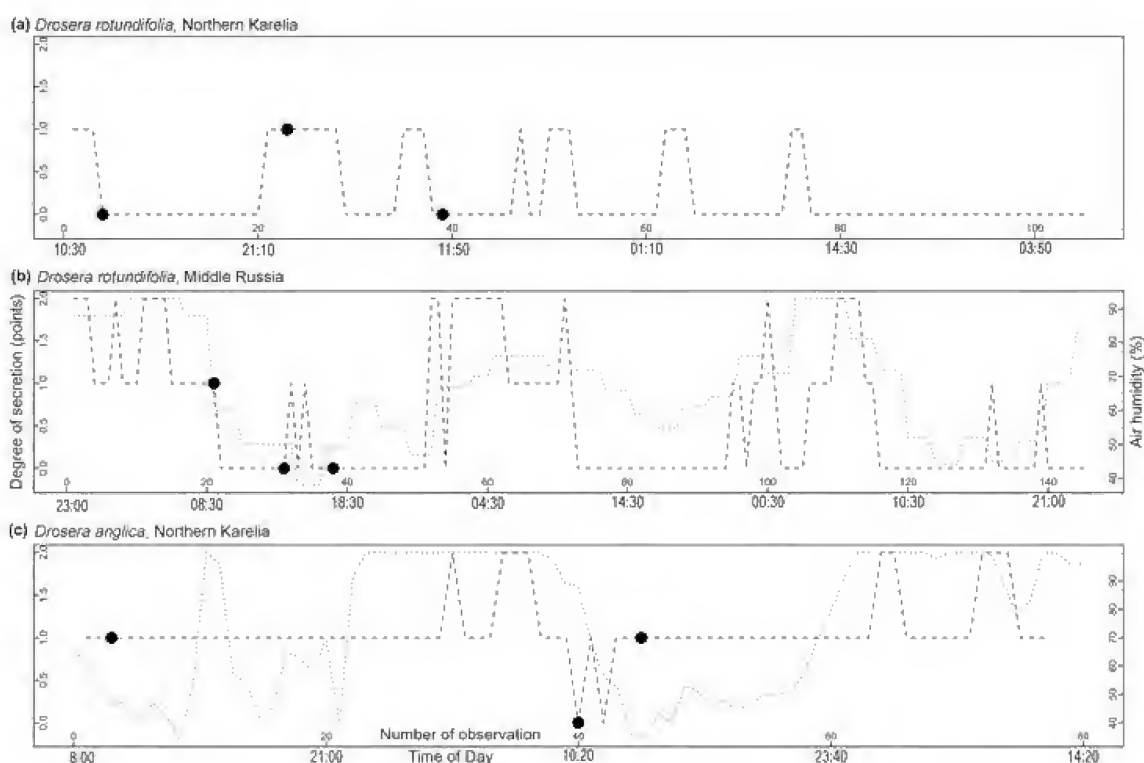


Figure 2: Changes in the degree of secretion of model *Drosera* leaves, compared with changes of relative air humidity. Relative air humidity (right Y-axis) is shown with the dotted line (not available for *D. rotundifolia* in Northern Karelia). The times of arrival of the fresh insect on the leaf blade are shown with filled circles.



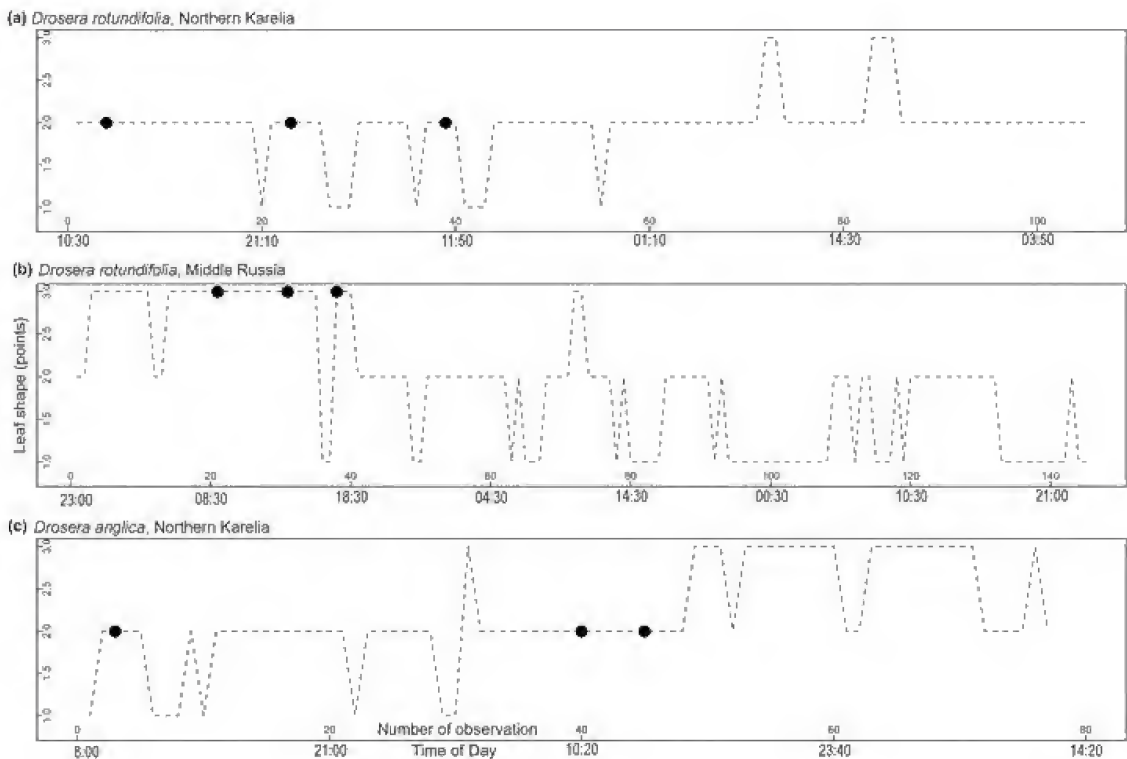


Figure 3: Changes in the shape of the model *Drosera* leaves. The times of arrival of the fresh insect on the leaf blade are shown with filled circles.

Differences between feeding strategies of *D. rotundifolia* and *D. anglica*, revealed by visual inspection of our data (Table 1), were illustrated with PCA (principal component analysis) of averaged behavior for all three species/region groups plus the “ideal” sundew (imaginary plant with maximal values of leaves characteristics in 1 hour after prey catching).

For statistical analyses and graph creation, R environment for statistical computing was used (R Development Core Team 2007).

## Results

A significant number of trapping leaves did not react to the prey in one hour: from 52% for *D. rotundifolia* in North Karelia to 29% for the same species in Tver region (45% for pooled data). These proportions were significantly different from the expectation of 95% change (Chi-square test  $p < 0.05$  for all four cases). In next two hours, leaf conditions did not change significantly: ANOVA analysis for 0.5, 1, 2, and 3 hour time shifts did not reveal any significant dependence between time and leaf characteristics (in all three cases  $p > 0.1$ ). In general, there were no significant differences between leaf condition at the moment of prey capture and in one hour later (Wilcoxon  $p > 0.1$  for all three leaf characteristics). Only degree of secretion, and only for plants from North Karelia demonstrated some significant differences (Wilcoxon  $p < 0.05$  for both *D. anglica* and *D. rotundifolia* from this region). At the same time, there was an evident relation between the degree of secretion and relative air humidity (see Figures 2 and 4; Spearman  $\rho = 0.37$ ,  $p < 0.05$ ; ANOVA  $p < 0.05$ ). Degree of bending and shape were correlated with humidity to a much lower extent (Spearman  $\rho < 0.1$  in both cases).

Quite often the behavior of leaves was different from that usually discussed in the literature (see Figures 1-3), or “ideal behavior” (to imitate this behavior, we used maximal values of leaf characteristics). As an example, all the leaf characters in 0.5-3 hours after prey capture differed significantly from “ideal” values (Wilcoxon  $p < 0.01$  for all leaf characteristics).

Leaf characteristics	Scores
Secretion degree	0 – poor, the leaf is almost dry 1 – medium 2 – high, droplets are well-formed
Leaf shape	1 – leaf is almost flat 2 – leaf is almost flexed 3 – leaf is almost bent
Degree of bending	1 – no or few bent tentacles 2 – approximately half of the tentacles are bent 3 – all or almost all tentacles are bent

Table 1: Leaf characters observed.

Characteristics of leaves without prey did not differ significantly from characteristics of leaves that caught prey 1 hour ago (Wilcoxon  $p > 0.1$ ) for all cases except degree of secretion for North Karelian plants (Wilcoxon  $p < 0.05$ ). In addition, leaves without prey often had the “wrong” condition: more than 44% of them have all three characteristics that deviated from condition “by default” (Chi-square  $p < 0.05$ ).

Changes of different types were not correlated – averaged coefficients of correlation between all the three leaf characters were lower than 0.33 (mean correlation 0.06). The correlation in behavior of all leaves from the same plant was low (Spearman  $\rho = 0.25$ ), but for bending and secretion of leaves belonging to *D. rotundifolia* from Tver region, values of correlation were higher than 0.4 and significant. Consequently, ANOVA analysis of correlation between years revealed a significant difference ( $p < 0.05$ ) whereas no differences in correlation coefficients were revealed from comparison of different characteristics from pooled data (ANOVA  $p \gg 0.1$ ) and from comparison of different plants observed in the same year (Wilcoxon paired signed rank test  $p \gg 0.1$ ).

For *D. anglica* the number of insects caught varied from 0 to 1.4 (0.6 in average) per leaf in a day, while *D. rotundifolia* trapped from 0 to 0.7 insects (0.3 in average) in the Northern Karelia, and from 0 to 3.0 (1.0 in average) in the Middle Russia. PCA analysis of one hour behavior for all three species/region groups revealed that *D. rotundifolia* plants from Moscow region behaved similar to *D. anglica* and *D. rotundifolia* from North Karelia. All three observations were distant from the “ideal” plant which differed from plants observed in nature by all three leaf characteristics. *Drosera rotundifolia* plants from North Karelia demonstrated more developed bending whereas *D. anglica* demonstrated more developed secretion (see Figure 5).

### Discussion

In all, our statistical analysis support the conclusion stated in our previous paper (Volkova & Shipunov 2005): secretion, leaf curving, and tentacle bending do not depend on prey capture, and secretion is probably regulated by relative humidity. Our results do not let us speculate about inconsistency between field and laboratory data. One possible reason could be that in artificial conditions sundew plants were simply overfed. Nevertheless, this inconsistency emphasizes the necessity of further investigation of trapping behavior of sundews.

The analysis also showed that differences between regions and between *D. anglica* and *D. rotundifolia* are almost equal. Despite the slightly different tactics, there is much more in common between the two studied *Drosera* species. This similarity could be caused by close genetic relationships between the two species (Rivadavia *et al.* 2003). The absence of correlation between the behavior of trapping leaves and presence of prey let us to consider sundew trapping leaves as a structure transitional between active and passive flypaper traps, whereas the common opinion con-



siders them as active flypaper traps (see, for example, Williams 1976; Heubl *et al.* 2006). Our data also support the recent hypothesis on the facultative role of carnivory in the carnivorous plants (Dore & Maham 1969; Small *et al.* 1977; Stewart & Nilsen 1992; Ellison & Gotelli 2001).

In general, it is possible to distinguish two main stages in every feeding process (Hardys *et al.* 1990): “catching” (binding of food with the feeding organ) and “digesting” (absorption of food). There are transitions between “poor catchers and digesters” as protocarnivorous plants (Spomer 1999) and “perfect catchers and digesters” as carnivorous plants with snap-traps (Heubl *et al.* 2006). Some primitive animals like *Hydra*, or *Eleutheria* appear to be “non-perfect catchers”, but “perfect digesters” (Lasker *et al.* 1982; Hardys *et al.* 1990). According to this classification, the two studied *Drosera* species in the Middle and Northern European Russia, being “non-perfect catchers and digesters”, have a separate feeding type which can be named as “semi-accidental feeding”.

In both non-animal carnivores, nematode-trapping fungi, and carnivorous plants, evolution of feeding structures have many common features (Mueller *et al.* 2004; Li *et al.* 2005; Heubl *et al.* 2006). In particular, primitive passive traps (passive fly-paper and adhesive knobs, respectively) evolved in two directions: perfect passive traps (pitfall traps and three-dimensional networks) and perfect active traps (snap and active flypaper traps and constricting rings). Since the flypaper traps of *Drosera* were likely derived from the ancestral passive traps, we can suppose that transition from passive to active traps happened within the *Drosera* genus, causing our two species with the semi-accidental feeding to be in the middle of this transition.

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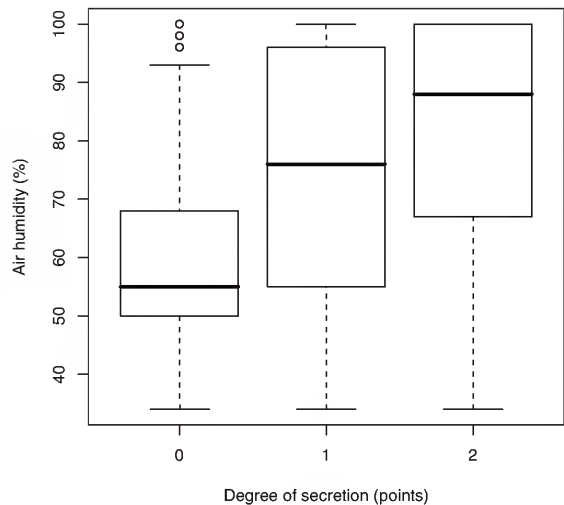


Figure 4: Box plot demonstrating the dependence between air humidity and degree of secretion (for all data).

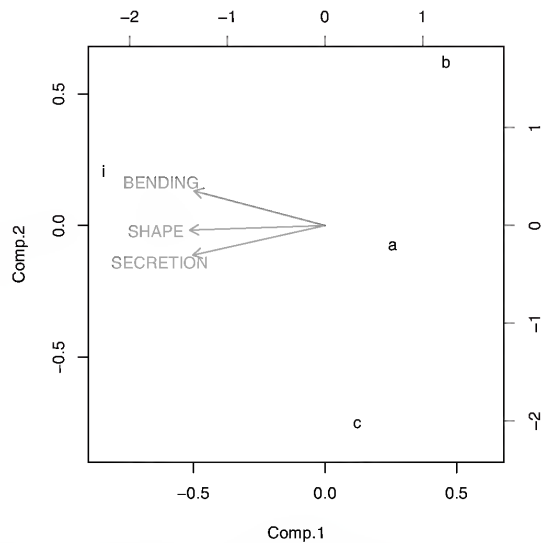


Figure 5: Biplot of the principal component analysis (PCA). Arrows represent character loading, points belong to the averaged one-hour behavior of each observed species/region, plus “ideal” sundew (imaginary plant with maximal values of leaves characteristics); a: *D. rotundifolia*, Northern Karelia; b: *D. rotundifolia*, Middle Russia; c: *D. anglica*, Northern Karelia; i: “ideal” plant.

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*DROSERA* × *FONTINALIS* (DROSERACEAE), THE FIRST NATURAL SUNDEW  
HYBRID FROM SOUTH AMERICA

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Introduction

Artificial *Drosera* hybrids are known from several subgenera and sections in the genus *Drosera*, such as *D. capensis* L. × *D. slackii* Cheek, *D. neocaledonica* R. Hamet × *D. aliciae* R. Hamet, *D. nidiformis* Debbert × *D. dielsiana* Exell & Laundon, *D. burmannii* Vahl × *D. sessilifolia* A. St.-Hil., *D. kenneallyi* Lowrie × *D. lanata* K. Kondo, *D. dichrosepala* Turcz. × *D. roseana* N.G. Marchant & Lowrie, *D. anglica* Huds. × *D. spatulata* Labill., *D. oblanceolata* Y. Z. Ruan × *D. capillaris* Poir., *D. macrantha* Endl. × *D. andersoniana* W. Fitzg. ex Ewart. & White, and even complex hybrids such as *D. (falconeri* K. Kondo & P. Tsang × *ordensis* Lowrie) × *D. (darwinensis* Lowrie × *falconeri*) (Kusakabe 1979; Snyder 2000; Ziemer 2002). A smaller number of natural hybrids are known, such as: *D. allantostigma* (N.G. Marchant & Lowrie) Lowrie & Conran × *D. omissa* Diels, *D. omissa* Diels × *D. pulchella* Lehm. (Lowrie & Conran 2007), *D. aliciae* × *D. glabripes* (Harv. ex Planch.) Stein (Gibson & Green 1999), as well as between most northern temperate taxa (Schnell 2002). Furthermore, a few *Drosera* species are almost surely of hybrid origin, such as *D. anglica* Huds. (Wood 1955) and *D. tokaiensis* (Komiya & Shibata) T. Nakamura & Ueda (Hoshi *et al.* 1994; Nakano *et al.* 2004).

In 1994 near the town of Grão Mogol in Minas Gerais state, southeastern Brazil, plants intermediate between *D. grantsau* and *D. tomentosa* were found at a site where both species were sympatric. Further studies showed these intermediate plants were present at numerous other localities where the two species grew sympatrically or in neighboring habitats in Minas Gerais, Goiás, and Bahia states. This is the first hybrid, natural or artificial, reported between native South American *Drosera* species (Rivadavia 2003, where *D. tomentosa* was treated as *D. montana* var. *tomentosa*). Its morphological and ecological characteristics are discussed below, with the help of illustrations and a distribution map.

Results

*Drosera* × *fontinalis* Rivadavia *hybrida nova*, *D. grantsau* Rivadavia × *D. tomentosa* A. St.-Hil. Type: Brazil, Minas Gerais, Grão Mogol, 9/Sep./1994, *Rivadavia* 302 (SPF) (see Figure 1).

*Drosera* × *fontinalis* Rivadavia, *hybrida nova*, *D. tomentosa* A. St.-Hil. × *D. grantsau* Rivadavia, *sed folia suberecta lanceolata, semina lacrymoidea*.

Perennial herbs with semi-erect leaves in rosettes (see Figures 3, 4). Stipules rectangular, membranaceous, translucent white to pinkish or bronze in color, 1.8-4.5 mm long and 0.5-1.6 mm wide at the base, the upper 1/2-1/3 divided into numerous filaments. Leaves green to wine-red in color, lanceolate, abaxially more or less sparsely eglandular-pilose to nearly glabrous; petioles 3-7 mm long and 0.5-1.0 mm wide, glabrous adaxially; lamina 4-11 mm long, 1-3 mm wide, adaxially covered with numerous retentive glands. Inflorescences erect, 1-3 per plant, 10-36 cm long (including

scape), rarely bifurcating at the apex, 2-12 flowers each, increasingly glandular-pilose (in number and size) towards the apex of the inflorescence, more or less eglandular-pilose on the lower half (or not at all), increasingly so (in number and size) towards the base of the scape; bracts ovate-filiform, 0.1-1.0 mm long, densely glandular-pilose and with rare eglandular hairs; pedicels 3-6 mm long, inserted 5-12 mm apart, glandular-pilose; sepals 5, oblong-ovate, 3-4 mm long, abaxially glandular-pilose, united at basal 1/4-1/5 of length; petals 5, obovate-cuneate, 4-6 mm long, light pink-lilac in

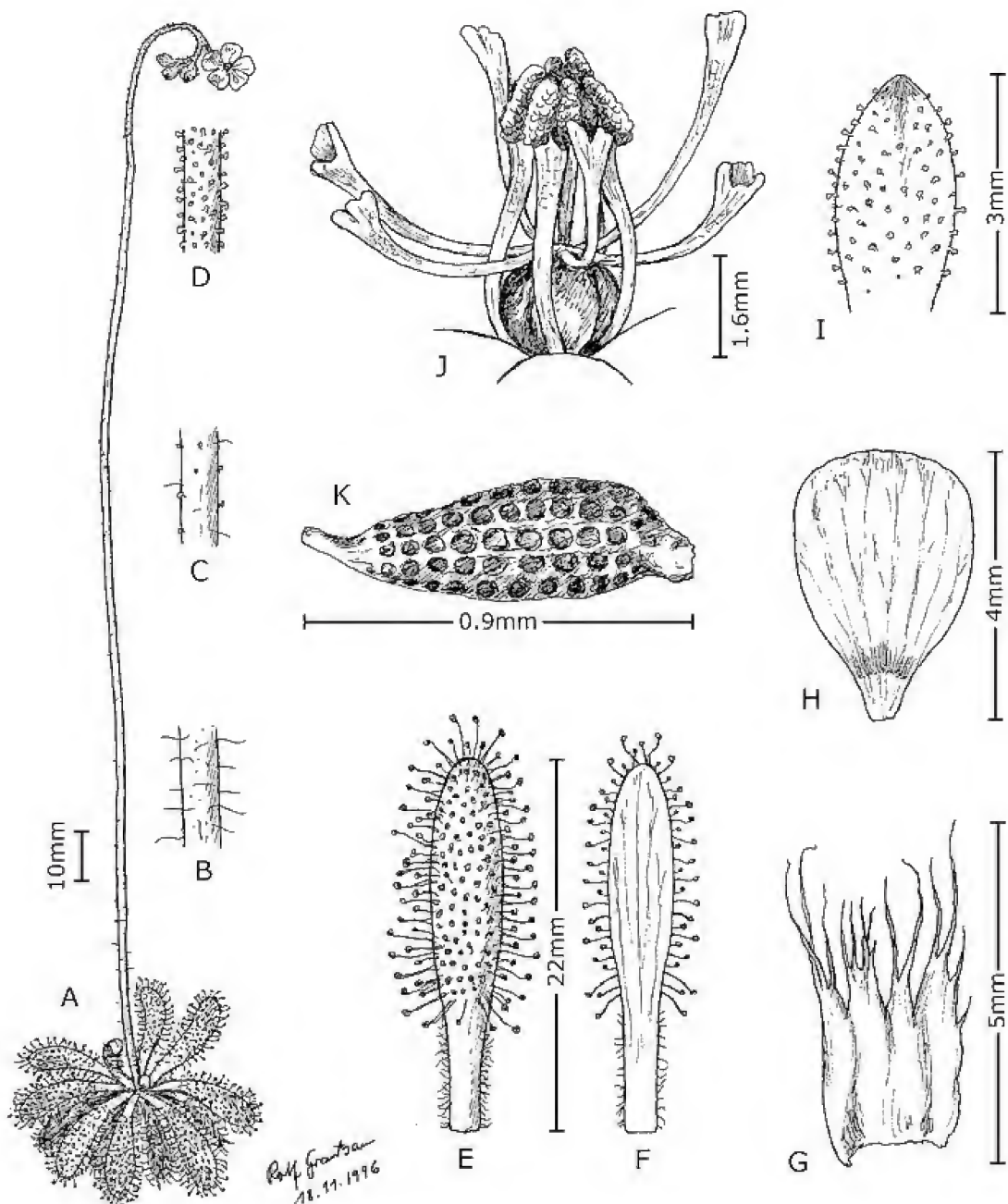


Figure 1: *Drosera x fontinalis* Rivadavia; A: habit; B: detail of indumentum near the base of the scape; C: detail of indumentum halfway up the scape; D: detail of indumentum on the upper portion of the scape; E: leaf, adaxial view; F: leaf, abaxial view; G: stipule; H: petal; I: sepal; J: gynoecium and stamens; K: seed. Based on cultivated live specimens from Itacambira, Minas Gerais (herbarium specimens from this location deposited at SPF: Rivadavia 309).



color; ovary ellipsoid-obovate, trilobed, 1.5-1.8 mm long at anthesis; carpels 3; styles 3, bifurcated at the base, 2-3 mm long, stigmata bilobed to flabellate and often cupped; stamens 5, 3 mm long, anthers 1.0-1.5 mm long; seeds black, lacrimoid, reticulated, 0.2-0.9 mm long and 0.05-0.1 mm wide (smaller ones appear to be undeveloped ovules).

*Specimens examined:* BRAZIL. Bahia: Abaíra, Catolés, Campo da Mutuca, 23/Mar./1992, Stannard & Silva 52793 (SPF) (mixed collection with *D. grantsau*); Abaíra, Catolés, trilha para o Campo da Mutuca, 29/July/1995, Rivadavia & Ganev 492 (SPF); Piatã, Serra do Santana, 13/Jul./2005, Rivadavia et al. 2004 (SPF). Goiás: Alto Paraíso de Goiás, estrada Brasília-A.Paraíso, 14/Apr./1995, Rivadavia & Ogassavara 382 (SPF); Alto Paraíso de Goiás, estrada A.Paraíso-Teresina de Goiás, 19/Mar./1997, Rivadavia 654 (SPF); Alto Paraíso de Goiás, estrada A.Paraíso-Teresina de Goiás, 23/Jun./2007, Rivadavia & Batista 2626 (SPF). Minas Gerais: Botumirim, Serra da Canastra, 21/Dec./1994, Rivadavia 340 (SPF); Botumirim, Serra da Canastra, 13/Oct./2001, Rivadavia 1272 (SPF); Grão Mogol, 7km ao sul da cidade, 15/Oct./1988, Harley et al. 25067 (SPF); Grão Mogol, Morro do Jambeiro, Rivadavia 286, 3/June/1994 (SPF); Grão Mogol, Rivadavia 292, 7/Sep./1994 (SPF); Grão Mogol, Morro do Jambeiro, 8/Sep./1994, Rivadavia 301 (SPF); Grão Mogol, 12/Oct./2001, Rivadavia 1262 (SPF); Itacambira, beirando a estrada M.Claros-Itacambira, 16/Dec./1994, Rivadavia 309 (SPF); Itacambira, estrada para M.Claros, 5/Mar./1997, Rivadavia 603 (SPF); Itacambira, estrada para M.Claros, 13/Oct./2001, Rivadavia 1291 (SPF); Joaquim Felício, Serra do Cabral, estrada entre J.Felício e Francisco Dumont, 3/July/2003, Rivadavia 1664 (SPF); Joaquim Felício, Serra do Cabral, a 22km de J.Felício, Rivadavia 1664, 3/Jul./2003 (SPF).

*Drosera* × *fontinalis* is morphologically most similar to *D. tomentosa* (see Figure 4), which differs in having leaves usually flat, oblong-obovate, petioles 0.4-3.0 mm (0.02-0.12 in) wide, lamina 1.3-6.0 mm (0.05-0.24 in) wide, and seeds more ovoid. The hybrid also resembles small specimens of *D. ascendens* A. St.-Hil., which differs in usually being much larger and more robust, but especially in its lacrimoid seed.

The distribution and length of eglandular hairs on leaves and inflorescences of the hybrid is variable from site to site, due to the fact that both *D. grantsau* and *D. tomentosa* are themselves extremely variable in this character. The inflorescence of *D. × fontinalis* may reach 36 cm (14 in) in length (Rivadavia 603 at SPF), which is longer than in any of the numerous dried specimens examined for both parental species (maximum of 26.5 cm (10.4 in) in *D. grantsau* and 33 cm (13 in) in *D. tomentosa*), showing a touch of hybrid vigor.

*Drosera* × *fontinalis* occurs in permanently wet to humid seepage habitats, sometimes on live *Sphagnum* spp., in boggy humus-rich soil, or in wet sand mixed with black peat. Similar to *D. tomentosa*, the hybrid is most often found in flower between the middle of the dry season and early in the wet season (approximately from June to November).

Large numbers of *D. × fontinalis* are often observed, at some places apparently more abundant than one or even both parental species. This suggests that either asexual reproduction may be common, possibly through the roots, or else *D. × fontinalis* may be fertile, although no seeds have germinated in cultivation. *Drosera* × *fontinalis* is especially abundant on highlands surrounding the three towns of Grão Mogol, Botumirim, and Itacambira (Minas Gerais) between c.700-1330 m (2300-4360 ft) altitude and on the northern part of the Chapada dos Veadeiros highlands (Goiás), at c.1400-1500 m (4600-4900 ft) altitude.

Although *D. tomentosa* is abundant throughout the Chapada Diamantina highlands (Bahia), *D. grantsau* is only known from two small populations near the towns of Catolés and Piatã, respectively at c.1550 m (5100 ft) and c.1370 m (4500 ft) altitude, where both species are sympatric and a small number of *D. × fontinalis* have been observed. On the Serra do Cabral (Minas Gerais), once again *D. grantsau* is only known from two small populations where it is sympatric with the more abundant *D. tomentosa*. Curiously, *D. × fontinalis* was only observed at the northernmost of the two locations, at c.1200 m (3950 ft) altitude.

Single small populations of *D. grantsau* surrounded by larger populations of *D. tomentosa*, but without any signs of *D. × fontinalis*, were also observed near Serranópolis (Minas Gerais), on the Serra do Cipó (Minas Gerais), on the Serra da Canastra highlands (Minas Gerais), and on the southern side of the Chapada dos Veadeiros.

Inexplicably, no *D. × fontinalis* plants have ever been observed in a wide area surrounding the town of Diamantina (including Gouveia, São Gonçalo do Rio Preto, and Milho Verde in Minas Gerais), where *D. grantsau* and *D. tomentosa* are abundant and frequently occur sympatrically. (see Figure 2)

The epithet “*fontinalis*” refers to the fact that *D. × fontinalis* was always found growing in natural springs, where water seeps continuously over wet soil.

Acknowledgements: I would like to thank Rolf Grantsau for the botanical drawings; Andreas

Figure 2: Map showing the known distribution of *Drosera × fontinalis* Rivadavia (x-symbols) and locations where the parental species have been observed, but no hybrids (filled triangles). Sites indicated on the map may represent more than one collection listed in this paper.

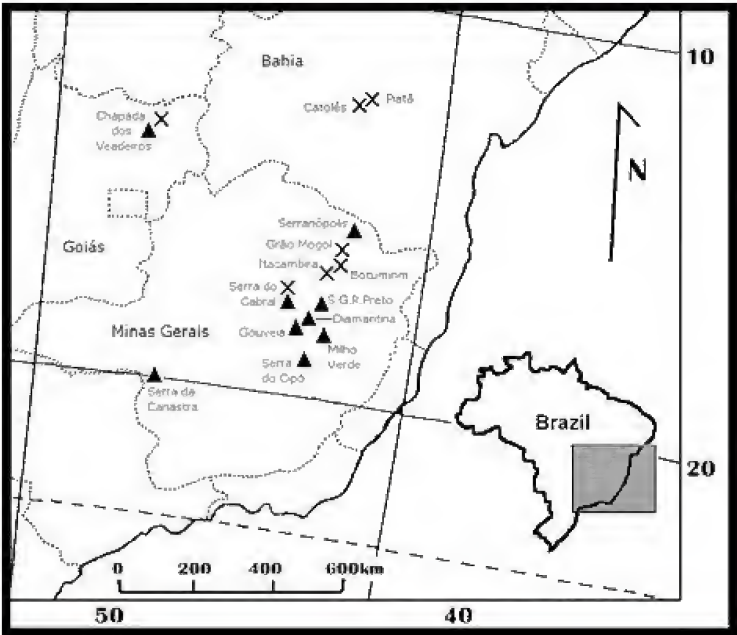


Figure 3: *Drosera × fontinalis* Rivadavia at the Chapada dos Veadeiros.





Figure 4: *Drosera tomentosa* A.St.-Hil. var. *tomentosa* (left) and *D. x fontinalis* Rivadavia (right) at Piatã, Chapada Diamantina. *Genlisea aurea* A.St.-Hil. can be seen in the background. Photograph by Ed Read.

Fleischmann for helpful comments and suggestions on this manuscript and for the Latin description; Paulo Gonella for help measuring, photographing, and organizing herbarium specimens; Ed Read for permission to use his photograph; as well as the many friends who joined me on numerous expeditions to study these plants in the field.

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## LITERATURE REVIEWS

By Doug Darnowski

Gibson, T.C., and Waller, D.M. 2009. Evolving Darwin's 'most wonderful' plant: ecological steps to a snap-trap. *New Phytologist* 183: 575-587.

In this review, the authors present a comprehensive picture of the probable steps in the evolution of the snap traps of *Dionaea* and *Aldrovanda* from the sticky traps of *Drosera*, with an emphasis on *D. regia*, the most primitive of the sundews and the closest living relative of the two genera which have snap traps. An impressive range of ideas are presented, from Darwin's musings through the most recent data on the ecological costs of carnivory from Ellison's lab. The paper includes extensive review of both molecular and morphological data, but the style is simple and lucid, so the text should be accessible for any ICPS member. While a fair amount of speculation still lies in the proposed evolutionary path, many ICPS members will find this a fascinating paper. (DWD)

Rivadavia, F., Vincentini, A., and Fleischmann, A. 2009. A new species of sundew (*Drosera*, Droseraceae), with water-dispersed seed, from the floodplains of the Northern Amazon Basin, Brazil. *Ecotropica* 15: 13-21.

Yet another fascinating species of South American carnivore comes from the work of Fernando Rivadavia and Andreas Fleischmann, an unusual lowland sundew, *Drosera amazonica*. It falls into section *Drosera*, and its closest relative is *D. felix*. It grows on seasonally-flooded white quartz sand, reminiscent of many carnivores, and, interestingly, its flowers have a sweet scent. Perhaps the most fascinating feature of *D. amazonica* is found in its seed, which have bumpy coats that catch air bubbles. These buoy the seeds and probably lead to dispersal of the seeds by water. (DWD)

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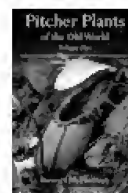
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